TOPICAL REVIEW

Saccades and pursuit: two outcomes of a single sensorimotor process

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Saccades and smooth pursuit eye movements are two different modes of oculomotor control. Saccades are primarily directed toward stationary targets whereas smooth pursuit is elicited to track moving targets. In recent years, behavioural and neurophysiological data demonstrated that both types of eye movements work in synergy for visual tracking. This suggests that saccades and pursuit are two outcomes of a single sensorimotor process that aims at orienting the visual axis.

(Received 2 July 2007; accepted after revision 6 August 2007; first published online 9 August 2007)
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When collaboration is required

In order to get clear vision of an object of interest, the projection of this object onto the retina must fall on the fovea, which is the region of the retina with the highest visual acuity. Therefore, in everyday life, humans orientate their visual axis to targets of interest that can either be stationary or moving. While scanning their environment, humans perform multiple saccades (rapid eye movements that correct for a position error between eye and target) to align their visual axis with objects of interest. Humans are also able to track objects that move in their environment by means of smooth pursuit eye movements (slow eye movements that stabilize the projection of the moving target onto the fovea and correct for any velocity error between eye and target, i.e. for any retinal slip).

The appearance of a moving stimulus in the environment elicits smooth pursuit eye movements with a latency of around 100 ms. Accordingly, the smooth pursuit system accounts for a change in the trajectory of a moving target with a similar delay. This delay is largely due to the early processing of visual inputs by the visual system and cannot be eliminated. Because of this inherent delay, large position errors arise during the visual tracking of a stimulus that changes its trajectory abruptly. Moreover, the maximum smooth eye velocity and acceleration that can be achieved is limited, i.e. the change in smooth eye velocity is not instantaneous. Consequently, smooth eye movements cannot reach large velocities in a short period of time and cannot track very fast targets (Fig. 1*A*), which results in an accumulation of position error. Due to these limitations, the oculomotor system needs to develop strategies to avoid the build up of position error during tracking of a moving target. To do so, the oculomotor system uses prediction to try and anticipate the future target trajectory during smooth pursuit eye movements (Fig. 1*B*; Dallos & Jones, 1963; Bahill & McDonald, 1983; Barnes & Asselman, 1991). However, this strategy is limited to conditions where target trajectory is predictable. In particular, it fails in all conditions where the target undergoes unpredictable changes in trajectory, as they cannot be anticipated by the subject. For instance, most people have probably experienced how difficult it is to track and catch a mosquito on-the-fly. Indeed, even though its velocity is low, the flight trajectory of a mosquito is very unpredictable. Thus, it is a very good example of a very frustrating condition (especially in the middle of a short night) of a task that seems quite easy due to the small velocity of the target but turns out to be very difficult because predictive mechanisms cannot be used. In sum, the smooth pursuit system cannot manage unpredictable or very fast moving targets on its own (Fig. 1*A* and *C*).

Therefore, primates do combine pursuit and saccades in visual tracking of unpredictable moving targets to avoid large position error and eye lagging behind the target (Fig. 1*C*). The execution of a saccade helps catching up with the target quickly (hence their name: catch-up saccades). In contrast with saccades towards stationary targets that only take the position error into account, catch-up saccades also need to consider the relative motion of the eye with respect to the object of interest to be accurate (de Brouwer *et al.* 2001). Besides, saccades deteriorate vision during their execution, i.e. large changes in the visual world occurring during saccades are not detected (Bridgeman *et al.* 1975). Thus, the oculomotor system faces

 DOI: 10.1113/jphysiol.2007.139881

a trade-off between short epochs of poor vision (due to catch-up saccades) and poor tracking (eye lagging behind the target).

In sum, the smooth pursuit system needs to collaborate with the saccadic system in order to improve tracking of a target that moves in an unpredictable way. The collaboration starts at the level of the visual inputs (position and velocity errors) that must be shared between both systems and at the level of the decision, i.e. whether an error must be corrected by the smooth pursuit system on its own or by a catch-up saccade. The two inputs are mediated by different brain pathways that were primarily attributed to only one of the oculomotor subsystems (position pathway to saccades and motion pathway to smooth pursuit). However, as we have emphasized in this introduction, saccadic and smooth pursuit systems work hand in hand to optimize visual tracking of moving targets. In this review, we will first describe the contribution of the motion and position pathways to both saccadic and smooth pursuit eye movements. We will then introduce the synergies developed by the brain to track moving targets in a very efficient way. Finally, we will present the neural substrate underlying the interaction between saccades and pursuit.

Both position and motion pathways contribute to saccades and pursuit

Contribution from the position pathway to the saccadic system. Saccades typically respond to a sudden step of the target and correct for the position mismatch between the visual axis and the object of interest (see Leigh & Kennard, 2004 for a review). Saccades are fast eye movements (up to 1000 deg s^{-1}) and their duration is very short (30–80 ms). Their peak velocity, duration and amplitude show consistent relationships (the main sequence, Bahill *et al.* 1975). On average, saccades undershoot stationary targets and only account for ∼90% of the distance between the eye and the target (Becker, 1991). As their duration is very short, saccades cannot be controlled by continuous visual feedback, which is characterized by a delay of around 100 ms, but instead by an internal feedback loop based on an efference copy of the motor command sent to the motoneurons (see Bridgeman, 1995 for a review).

From the visual input to the motor command generating the saccade, the position signal undergoes a sensorimotor transformation that consists of mapping the position error vector to a motor command, which is then sent to the extra-ocular muscles. This sensorimotor transformation, which underlies the generation of the saccades, is subserved by a cortical network (Leigh & Zee, 2006) consisting of the saccadic part of the frontal eye fields (FEF), the supplementary eye fields (SEF) and the lateral intraparietal area (LIP). The cortical eye fields project to the brainstem, to the superior colliculus (SC), either directly or through the basal ganglia, and to pontine nuclei which relay the information to the saccadic region of the cerebellum (dorsal vermis and fastigial nucleus). The SC, which contains a retinotopic map of the visual field, codes the position error signal. Both the cerebellum

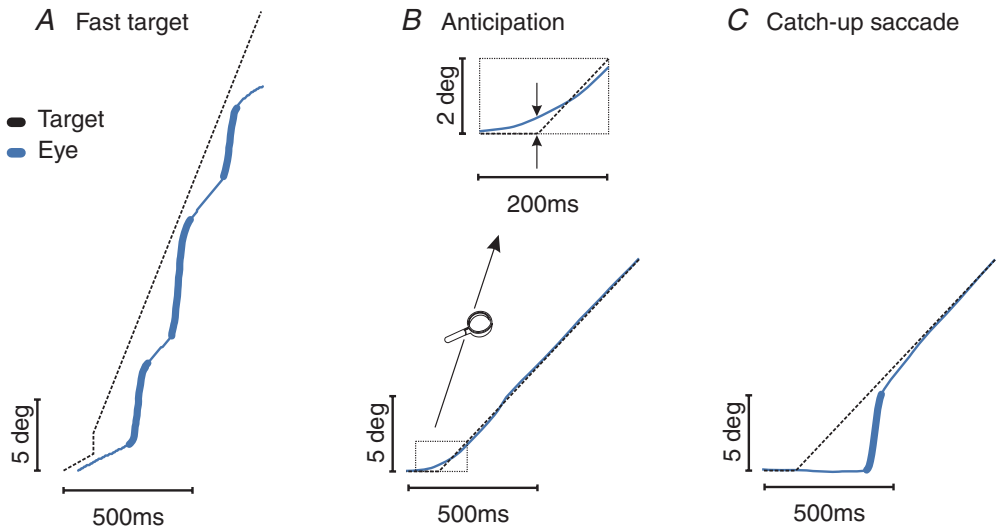

Figure 1. Oculomotor strategies in visual tracking
For each panel, eye and target position are represented *versus* time. *A*, the eye velocity saturates and cannot match target velocity. Therefore, catch-up saccades are triggered (thick traces). Target velocity is 50 deg s^{-1}. *B*, the oculomotor system predicts the time of target motion onset and the eyes begin to move before the target does. The inset provides a zoom around target motion onset. The arrows highlight the advance in position of the eye with respect to the target at its onset. *C*, a catch-up saccade (thick blue trace) is executed to suppress the position error around 200 ms after target motion onset. For *B* and *C*, target velocity is 18 deg s^{-1}.

and the SC project to the premotor circuit located in the brainstem that sends the command to the ocular motoneurons (see Ramat *et al.* 2007 for an overview of the brainstem circuitry).

Contribution from the position pathway to the smooth pursuit system. As the retinal position of the target influences the eye acceleration just after pursuit onset (Lisberger & Westbrook, 1985), several experiments were designed to assess the contribution of the position pathway to the smooth pursuit system in primates. For example, a sudden jump of the target during motion elicits a change of the smooth eye velocity to correct for position error (Carl & Gellman, 1987; Segraves & Goldberg, 1994). Moreover, the stabilization of the target onto the retina with a small offset with respect to the fovea elicits smooth pursuit eye movements that aim to correct for the artificially created position error (Wyatt & Pola, 1981; Morris & Lisberger, 1987; Barnes *et al.* 1995). However, these experiments have been largely ignored for years, partly because they could only bring indirect evidence of a position input to the smooth pursuit system and could be influenced by concurrent retinal slip. In contrast, experiments in the cat shed light on how the position pathway influences smooth pursuit and which brain structures mediate this influence.

Saccades in cats are rather inaccurate in comparison with saccades in primates and are characterized by a much lower and variable gain. Therefore, when cats orientate their visual axis towards an eccentric target, they usually perform multiple saccades interleaved with slow eye movements towards the target (Missal *et al.* 1993). These slow eye movements were the first evidence in the cat of a contribution of the position pathway to the smooth pursuit system, which was consistent with modelling studies (Lefevre & Galiana, 1992; Lefevre *et al.* 1994). In addition, stimulation in the SC, which is part of the position pathway, evokes smooth eye movements in the cat (Missal *et al.* 1996, 2002*b*).

Finally, as a proof of a direct position input to the smooth pursuit system in primates, smooth eye movements were elicited towards a target that was briefly flashed aside the path of an ongoing moving target that was being tracked (left panel of Fig. 2, Blohm *et al.* 2005*b*). Importantly, this only occurs when the flash is a relevant target and not if it is a distractor. In addition, the smooth eye velocity elicited by such a flash is modulated by the amplitude of the position

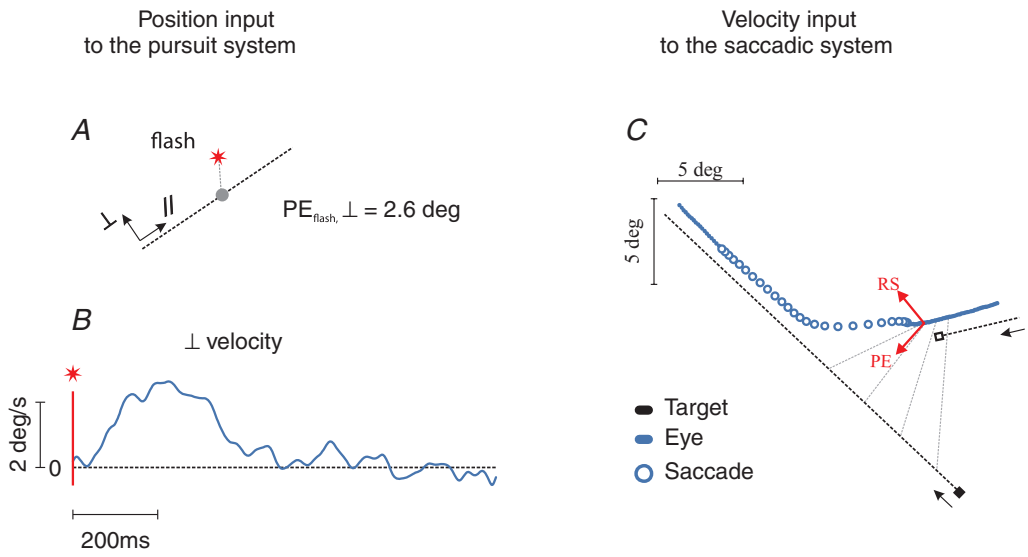

Figure 2. Position input to the smooth pursuit system and velocity input to the saccadic system
A, schematic representation of the protocol: the target follows a linear path and a second target (red star) is flashed during ongoing smooth pursuit. The position of the moving target at the time of the flash is represented by the grey disk. For the illustrated trial, the target velocity is 27 deg s^{-1} along the // axis. The target is flashed for 10 ms at 2.6 deg perpendicularly to the target path (along the ⊥ axis). *B*, representation of the eye velocity perpendicular to the target trajectory (⊥ axis) *versus* time. Eye velocity perpendicular to the target path increased after the apparition of the flash (red vertical line). *C*, a curved saccade (blue circles) occurring after both position and velocity steps of the target (black dashed lines) is presented in two dimensions. Target positions just before and after the target step are represented by the open and closed squares, respectively. Before and after the saccade, smooth pursuit eye movements (continuous blue lines) are present to track the target. The grey dotted lines represent isochronic lines that connect eye and target at the same moment in time. Red arrows give the position error (PE) and retinal slip (RS) orientation before the saccade. The saccade is elicited with an initial orientation close to the orientation of PE and final orientation close to the orientation of RS.

error, i.e. the larger the distance between the flash and the eye, the larger the smooth response heading toward the flash.

In summary, the position pathway contributes both to the saccadic and the smooth pursuit system. This contribution is preponderant in the case of the saccadic system and is less prevalent in the case of the smooth pursuit system as position error is generally not sufficient to elicit robust smooth pursuit eye movements.

Contribution from the motion pathway to the smooth pursuit system. The motion pathway contributes to the execution of smooth pursuit eye movements in order to stabilize the visual axis on the object of interest (see Thier & Ilg, 2005 for review). The smooth pursuit eye movements are elicited by retinal slip (or velocity error) but are also modulated by position (see previous section) and acceleration errors (Krauzlis & Lisberger, 1994). They cannot be performed at will but require the percept of a moving visual stimulus (Steinbach, 1976; Braun *et al.* 2006). Classically, the smooth pursuit system is presented as a closed loop system with a negative feedback of the eye velocity (Robinson *et al.* 1986). During the first 100 ms of pursuit, the smooth eye movements are considered as open-loop, before visual feedback closes the loop (Lisberger *et al.* 1987). Moreover, an online gain mechanism regulates the smooth pursuit system (Churchland & Lisberger, 2002). This gain is set to zero during fixation and to around one during visually guided pursuit. It is regulated by the pursuit region of the FEF (Tanaka & Lisberger, 2001).

Smooth pursuit eye movements are subserved by a cortical network involving the medial temporal area (MT), the middle superior temporal area (MST) and the pursuit subregion of the FEF (Leigh & Zee, 2006). These regions project to the pontine nuclei that relay the information to the cerebellar cortex (dorsal vermis, flocculus and paraflocculus). The cerebellar nuclei (fastigial and medial vestibular) receive inputs from the cerebellar cortex and transmit the information to the ocular motoneurons. It is worthwhile to stress the importance of MT within this network (Born & Bradley, 2005). Indeed, MT codes both the velocity (Priebe *et al.* 2001; Priebe & Lisberger, 2004) and the acceleration (Lisberger & Movshon, 1999; Price *et al.* 2005) of the target. Stimulation of MT disrupts target motion perception (Komatsu & Wurtz, 1989) but motion perception has been reported in the absence of MT activity (Ilg & Churan, 2004). Moreover, lesions of MT abolish smooth pursuit eye movements (Dursteler & Wurtz, 1988). In sum, MT is the motion processor and feeds the network with the motion signal.

Contribution from the motion pathway to catch-up saccades. As we emphasized in the introduction, catch-up saccades are necessary to overcome the limitations of the smooth pursuit system. They superimpose their response to the smooth pursuit response (de Brouwer *et al.* 2002*a*) and greatly improve the tracking of a target that moves unpredictably. Cats particularly need these catch-up saccades because their smooth pursuit gain is low and more variable that in humans (Missal *et al.* 1995; de Brouwer *et al.* 2001).

Catch-up saccades do differ from saccades towards stationary targets, as their main sequence is different (de Brouwer *et al.* 2002*a*). Their amplitude is not related to the position error only (Keller & Johnsen, 1990; Gellman & Carl, 1991; Kim *et al.* 1997) because if it were the case, saccades directed towards a moving target would always fall short. Therefore, the motion of the target must be taken into account in the programming of saccade amplitude. Catch-up saccade amplitude is programmed using both the position error and the retinal slip, i.e. the amplitude of catch-up saccades is the sum of a term related to the position error plus a term related to the prediction of the relative motion of the eye with respect to the target (de Brouwer *et al.* 2001). The existence of these two separate components is confirmed by their different neural substrate. The term related to the position error is coded in the SC that lays in the position pathway (Keller *et al.* 1996*b*). In contrast, the term related to the velocity error originates from the motion pathway. Indeed, when MT is lesioned, saccades made to stationary targets are normal (position pathway is intact) but catch-up saccades are not (motion pathway is disrupted, Newsome *et al.* 1985; May *et al.* 1988).

The outputs of these two pathways are not synchronized: the position error influences the saccade first. This asynchrony can yield curved catch-up saccades where the initial orientation of the saccade is correlated with the orientation of the position error and the final orientation of the saccade is correlated with the velocity error orientation (right panel of Fig. 2, Schreiber *et al.* 2006). Similarly, in one dimension, the asynchrony implies that the motion pathway mainly influences the deceleration phase of the catch-up saccades, not their acceleration phase (Guan *et al.* 2005). As a result, the velocity profiles of catch-up saccades are more skewed and variable than the profiles of saccades made to stationary targets.

Importance of studying visual tracking across different species. A historical perspective on the progress made in the last decade on the interaction between saccades and pursuit clearly demonstrates the critical importance of studying similar tasks across species. In particular, the apparent limitations of the oculomotor system in the cat (limited oculomotor range, undershooting saccades and saturation of smooth pursuit velocity) turned out to be a critical feature in our understanding of the interactions between saccades and pursuit. Indeed, when

the performance of a system is less efficient, as it is the case in the cat compared with the monkey, the synergy between the different subsystems becomes vital. This explains why the observation of the influence of position error on smooth pursuit (Missal *et al.* 1993, 1996; Lefevre *et al.* 1994) and velocity error on catch-up saccades (de Brouwer *et al.* 2001) is more obvious in cats. Thus, their investigation in the cat was a critical step to design experiments addressing the same questions in primates.

Synergies

The saccadic and smooth pursuit systems share the same inputs, i.e. the position and motion inputs. In this section, we will review how these inputs are combined in order to align the visual axis with the target for both types of eye movements.

Trigger mechanism of catch-up saccades. In the introduction, we have shown that the smooth pursuit system needs help from the saccadic system to track accurately a moving target. Indeed, when a target starts moving, position error is accumulating because of the latency of smooth pursuit eye movements (Fig. 1*C*). Therefore, the oculomotor system generates a saccade to compensate for this position error. Similarly, the smooth pursuit system fails to increase the eye velocity to match the velocity of very fast moving targets (Fig. 1*A*). In this case, catch-up saccades are triggered to compensate for the accumulation of position error due to the retinal slip. In sum, both position error and retinal slip can elicit catch-up saccades during smooth pursuit eye movements.

The combination of position error and retinal slip can also prevent the execution of catch-up saccades because the oculomotor system anticipates that the future target motion will decrease the current position error. For example, if the target steps in one direction (say leftward) before moving in the other direction (say rightward), the oculomotor system predicts that the rightward target motion will reduce the leftward position error (this typical motion of the target is called the Rashbass paradigm). Therefore, the probability of observing a catch-up saccade can be very low if the size of the step is adapted to the target velocity (Rashbass, 1961). The probability of occurrence of a catch-up saccade is minimized when the target crosses its initial position 200 ms after the step (Carl & Gellman, 1987). In contrast, when a target begins to move abruptly, the probability of observing a saccade is very high (Fig. 1*C*). This example shows that when the brain predicts that the target trajectory will cross the eye position in a near future, no catch-up saccade is triggered because target motion per se will reduce the position error. In sum, triggering a saccade depends on the relative motion of the eye with respect to the target and is therefore related to the prediction of the future position of the target.

During foveal pursuit, the relative motion of the eye with respect to the target can be quantified by a parameter, the eye-crossing time, which corresponds to the time-to-contact between eye (visual axis) and target (de Brouwer *et al.* 2002*b*). The eye-crossing time is the time that the eye would need to catch the target on the basis of the extrapolation of its current motion (Fig. 3*A*). It is computed by dividing the opposite of the position error between eye and target by the relative velocity of the eye with respect to the target (retinal slip). When the eye-crossing time is outside the smooth zone (< 40 ms or > 180 ms), the decision to trigger a catch-up saccade is taken and a saccade is executed around 125 ms later (Fig. 3*B* and *C*). However, as long as the eye-crossing time remains within the smooth zone, the smooth pursuit system can correct for the error by modulating the smooth eye velocity (Fig. 3*D*).

In summary, during ongoing tracking of a moving target, the oculomotor system tries to optimize the visual feedback of the object of interest by using both the saccadic and the smooth pursuit system in synergy. Somehow, it could be hypothesized that the brain tries to minimize the cost of foveating the target, which is a combination of sensory costs. Indeed, executing a saccade alters vision (cost related to saccade execution) whereas holding a saccade increases the cost related to poor vision (cost related to misalignment between the eye and the target). Within this context, saccade triggering can be interpreted as an optimal control problem, similar to the ones solved by the brain in the control of our actions (Harris & Wolpert, 1998; Todorov & Jordan, 2002; Todorov, 2004; Harris & Wolpert, 2006). In this particular case, the outcome of this optimal control problem would consist of inhibiting saccades only for a specific range of eye-crossing times.

Extraretinal interactions. The trigger mechanism of catch-up saccades is based on sensory inputs coming from the position and motion pathways. However, in some cases, the saccadic and smooth pursuit systems can cooperate despite the absence of retinal signals. In this case, internal models and efference copies provide the oculomotor system with an estimation of the position and velocity signals.

For instance, when an ongoing pursuit target is temporarily occluded (Fig. 3*E*), the decrease in the smooth pursuit response is compensated by the release of one or several saccades during the occlusion in order to maintain the performance of the oculomotor system (Mitrani & Dimitrov, 1978; Becker & Fuchs, 1985; Masson & Stone, 2002; Bennett & Barnes, 2003; Churchland *et al.* 2003; Madelain & Krauzlis, 2003; Bennett *et al.* 2007). Interestingly, these saccades are scaled to the reduction in smooth eye velocity, demonstrating that efference

copies provide information about ongoing smooth pursuit response to the saccadic system (Orban de Xivry *et al.* 2006). In addition, when a target is flashed either during anticipation of a pursuit target (Blohm *et al.* 2003*a*) or during ongoing pursuit of a moving target (Blohm *et al.* 2005*a*), the oculomotor system is able to direct the visual axis towards the flashed target position (Fig. 3*F*). Localization of the flashed target is accurate even though it has been reported that the so-called flash-lag effect (Nijhawan, 1994) can alter the memorized position of the flash (Blohm *et al.* 2003*b*). Again, to orientate to the remembered target position, the saccadic system

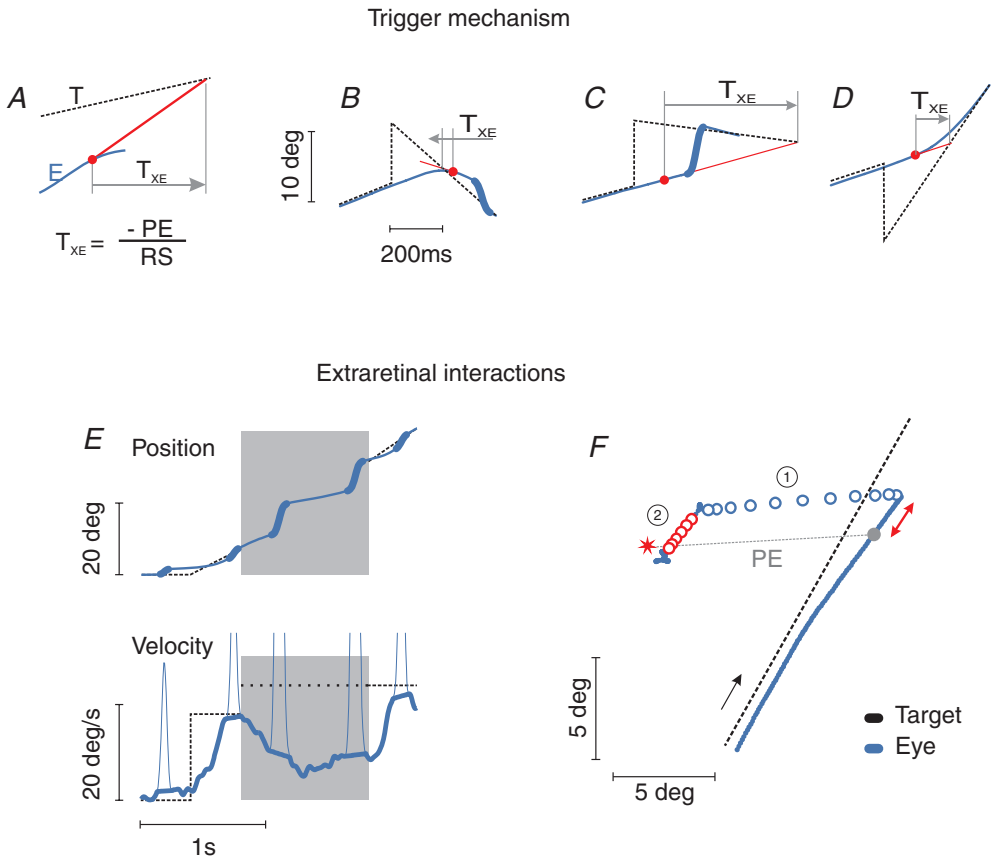

Figure 3. Trigger mechanism and extraretinal interactions
A, illustration of the eye-crossing-time parameter which corresponds to the time that the eye trajectory would need to cross the target at constant velocity (position *versus* time representation with T: target; E: eye; PE: position error; RS: retinal slip; T_{xe}: eye-crossing-time). To evaluate the eye-crossing-time at a certain instant in time (red dot), we compute the tangent to the eye trace (red line). The distance from the defined instant in time and the intersection between target and tangent yields the eye crossing time. *B*, *C* and *D*, representation of eye and target position *versus* time for three different trials that illustrate the trigger mechanism of the catch-up saccade (thicker traces). About 100 ms (red dots) before the saccade, we have represented the eye-crossing-time parameter following the definition in *A*. In trials *B* and *C*, the eye-crossing-time is outside the smooth zone (*B*: < 40 ms and *C*: > 180 ms). For trial *D*, there is no saccade because the eye-crossing-time remains within the smooth zone. *E*, illustration of the compensation for a decrease in the smooth eye velocity by the saccadic system during the occlusion of a pursuit target. The upper panel represents position *versus* time while the lower panel gives the velocity *versus* time. During the occlusion (grey areas), the smooth eye velocity tends to decrease (thick blue trace on velocity panel). To compensate for this decrease, saccades are generated during the occlusion (thick blue traces on the position panel). The collaboration between saccades and pursuit yields a small position error at target reappearance (at the right of the grey area on the upper panel). *F*, representation of how the saccadic system can integrate the smooth eye velocity to account for the smooth eye displacement while localizing a stationary target (same protocol as in Fig. 2: position input to the smooth pursuit system). During ongoing pursuit (continuous blue line for the eye and dashed black line for the target), a second target is flashed (red star). The position of the eye at the time of the flash is represented by the grey disk. A first saccade (blue circles) is triggered with a short latency toward the flashed target and the saccade vector matches the position error at the instant of the flash (grey dashed line). Subsequently, a second saccade (red circles) is triggered and accounts for the smooth eye displacement (SED, red arrow) following the flash.

must have access to an efference copy of the ongoing smooth eye movement and integrate it to compensate for the smooth eye displacement (Blohm *et al.* 2006). Interestingly, the extra-retinal information related to the relative motion of the eye with respect to the target is not available at very short latency but takes some time to be reconstructed. A direct consequence of this dynamical process is that the longer the reaction time the more accurate the eye movement. These experiments emphasize that the oculomotor system can increase its performance by cooperation between its two subsystems on the basis of extraretinal signals.

Initiation. Before executing an eye movement, the oculomotor system must first detect the target within the environment and program the motor command that will be sent to the ocular motoneurons. These two steps take some time and impose a delay (latency) between the appearance of the target and the execution of the eye movement. Interestingly, saccades and pursuit do not have the same latency (100 ms for pursuit and 200 ms for saccades) but their latencies vary in a similar way with the protocol being used. For instance, the latency of both types of eye movements decreases when the fixation point is extinguished a few hundreds of milliseconds before the target appears (gap effect; for saccades: Fischer & Boch, 1983; Merrison & Carpenter, 1995; for pursuit: Knox, 1996) by the same amount (around 50 ms, Krauzlis & Miles, 1996*a*,*b*). Neuronal correlates of the gap effect have been found in SC where the buildup activity that occurs before eye movements increases during the gap whatever the type of eye movement that will follow (Krauzlis, 2003). Similarly, the latency of saccades and pursuit increases in the presence of a distractor (Krauzlis *et al.* 1999). Although the latency of saccades and pursuit are quite different in response to the sudden appearance of a stimulus, they become comparable and highly correlated when the target appears before the disappearance of the fixation point (overlap protocol, Erkelens, 2006). Finally, both pursuit and saccades exhibit a similar dependence on movement preparation time, i.e. their latency exhibits a similar sharp transition between the reactive and predictive responses (Joiner & Shelhamer, 2006).

Thus, the protocol being used has similar influence on the latency of saccades and pursuit. This points to a common decision process to generate both types of eye movement. This process should account for the gap and overlap effects but also for the saccade latency variability that follows a recinormal (inverse Gaussian) distribution. For saccades, a linear rise to threshold model was proposed to account for the features of the saccadic latency (LATER model, Carpenter & Williams, 1995), i.e. the decision to trigger a saccade is taken as soon as a decision signal, starting from an initial level, reaches a particular decision threshold. The rate of rise of the decision signal is not fixed but follows a Gaussian distribution, which explains the recinormal distribution of the saccade latency (Carpenter & Williams, 1995). Recently, evidence showed that the decision signal is common to both saccades and pursuit but the decision thresholds are not, the saccadic threshold being higher than the pursuit threshold (Krauzlis *et al.* 1999; Krauzlis & Dill, 2002). The LATER model can account for the gap effect if it is assumed that the gap increases the initial level of the decision signal. Therefore, the time to reach the thresholds is decreased by the same amount for saccades and pursuit. This model nicely mirrors observed behaviour but it relies on the hypothesis that both saccades and pursuit initiation follow a LATER process. However, until now, it has never been reported that a LATER process underlies the generation of smooth pursuit eye movements, though a common initiation process has been shown.

Target selection. Initiation of an eye movement occurs after the presentation of an object toward which the gaze needs to be orientated. However, when multiple targets are presented simultaneously, the target of interest must first be selected before an eye movement can be initiated. As the initiation mechanism is shared between saccades and pursuit, we expect a single target selection mechanism to subserve both saccades and pursuit.

When two stimuli (one target and one distractor) moving in opposite directions are presented, smooth pursuit and saccades tend to select the same target, even if they choose the distractor (Krauzlis *et al.* 1999). Due to the difference in latency between saccades and pursuit, smooth pursuit eye movements are initiated first toward the selected target. On some occasions, when the smooth pursuit system selects the wrong target, a correction can occur on line in such a way that, at the time of the saccade, both pursuit and saccadic systems have selected the same target (Liston & Krauzlis, 2003). In this case, the saccade is delayed until corrective pursuit occurs. In summary, the state of the target selection mechanism is used early by the smooth pursuit system at the expense of the accuracy while the saccadic system waits longer to elicit a saccade directed to the target at the expense of the latency. So target selection takes place in the common preparatory stage and reflects a trade-off between speed and accuracy; the smooth pursuit system favours the speed because it can be corrected online whereas the saccadic system favours the accuracy because a saccade cannot be corrected on-the-fly. Interestingly, it has also been demonstrated that the execution of a saccade has a strong influence on the high-level motion processes involved in motion perception in the vicinity of the selected target (Gardner & Lisberger, 2001; Schoppik & Lisberger, 2006; Wilmer & Nakayama, 2007).

These behavioural data suggest that both subsystems share the same decision signal (race model). The race

model (Logan *et al.* 1984; Osman *et al.* 1986; Hanes & Schall, 1995; Hanes & Carpenter, 1999) consists of a decision signal that fluctuates between two thresholds, one for each stimulus. As soon as the decision signal reaches one of the two thresholds, an eye movement is made toward the corresponding target. However, the thresholds for the pursuit target selection and the saccade target selection are different, which means that overall, there are four thresholds for two potential targets: one for the pursuit and one for the saccade for each stimulus. The pursuit thresholds are lower than the saccade thresholds (Liston & Krauzlis, 2005), which can reflect the differences observed in the trade-off between speed and accuracy. The decision signal reaches a pursuit threshold faster but reaching the saccade threshold means that the system has accumulated more evidence (i.e. the confidence in the selection is higher).

The superior colliculus has a prevalent role in the common mechanism of target selection as its neuronal activity allows the prediction of target selection for both pursuit and saccades (Krauzlis & Dill, 2002). Furthermore, the stimulation of neurons in SC biases the target selection process in favour of the contralateral target whatever the planned eye movement, which suggests a causal role of SC in the target selection process (Carello & Krauzlis, 2004). The observed bias is related to the location of the target, not to its direction, which can be linked to the primacy of spatial information on target selection for both oculomotor systems (Adler *et al.* 2002). Regarding the hypothesized mechanism of target selection (common decision signal and different thresholds for pursuit and saccades), the stimulation of neurons in SC induces a bias of the initial level of the decision signal toward the contralateral target (Carello & Krauzlis, 2004). Hence, the duration needed to cross the pursuit and saccade thresholds is shorter (longer) for the contralateral (ipsilateral) stimulus in stimulated trials (Carello & Krauzlis, 2004). In summary, saccades and pursuit share a common target selection mechanism that is based on a race model. Neuronal correlates of this common mechanism can be found in the SC.

Cancellation of an eye movement. The sudden appearance of a novel object in the environment can require the inhibition of the planned action as circumstances that led to its planning have changed. Cancellation is often tested by the presentation of a stop-signal just before the initiation of the prepared saccade (Hanes & Schall, 1995; Hanes & Carpenter, 1999) or smooth pursuit eye movement. The success of the cancellation depends on the delay between the presentation of the stimulus and the stop-signal (Logan *et al.* 1984). An eye movement can easily be cancelled if this delay is close to zero. Accordingly, the longer the delay, the less successful is the stop-signal. Nevertheless, it takes an additional 20 ms to cancel a saccade (75 ms) in comparison with the cancellation of a smooth pursuit response (55 ms) (Kornylo *et al.* 2003). It has been suggested that this additional delay of 20 ms is inherent to the existence of a period of 20 ms before the saccade during which it cannot be aborted anymore. This observation is related to processes that precede saccade onset too closely to have an inhibitory influence (point of no return, Osman *et al.* 1986). A similar period does not exist for smooth pursuit. In summary, saccades and pursuit share a common cancellation mechanism even though the minimum period to cancel a saccade or smooth eye movement differs due to the existence of a point of no return for saccades but not for smooth eye movements.

The neural substrate of the cancellation mechanism is probably located in the brainstem premotor circuit, which is known to generate and control saccades. Within this premotor circuit, omnipause neurons (OPNs) inhibit the release of saccades and pause during their execution (Ramat *et al.* 2007). The existence of a common mechanism for eye movement cancellation is supported by the modulation of OPNs during both types of eye movements and the fact that their electrical stimulation interrupts saccades and reduces ongoing smooth eye velocity (Keller *et al.* 1996*a*; Missal & Keller, 2002).

Model. In summary, saccades and pursuit do share common inputs and their outputs are coordinated in order to optimally track the target. The described synergies are summarized in Fig. 4*A*. When the target is visible, retinal inputs are used to estimate both position error and retinal slip (RS, i.e. velocity error). When retinal inputs are not available (e.g. temporary occlusion of the target), these inputs are estimated by means of efference copies. In this case, RS is estimated from the efference copy of the smooth pursuit response combined with an estimation of target velocity, whereas position error is assessed by combining efference copies from both the saccadic and smooth pursuit systems together with an estimate of target parameters. These estimates are then processed into commands for saccades and pursuit and the decision is made to select one of the two modes of control (trigger). When a catch-up saccade is released, its motor command is added to the ongoing smooth pursuit command at the premotor level. The initiation, target selection and cancellation mechanisms, which are not represented in the figure, gate the execution of saccades and pursuit in parallel to the input processing (Krauzlis, 2005).

Brain areas subserving saccades and pursuit

Classically, neuroscientists considered that the position pathway fed the network subserving saccades whereas the motion pathway fed the smooth pursuit system with little if any interaction between the two systems and

their sensory inputs. However, the recent behavioural evidence described in the previous sections contradicts this view and suggests that both pathways influence both oculomotor subsystems (Fig. 4*A*). Somehow, the experimental evidence of the integration of the position and motion signals has changed the view of the neuronal network subserving the oculomotor system from two segregated networks into intertwined ones (Fig. 4*B*).

The brain networks subserving the oculomotor system originate at the level of the retinal inputs. These inputs are then spread into two parallel cortical pathways, subserving mainly the saccadic or the smooth pursuit system. Within these pathways, the frontal and supplementary eye fields (FEF and SEF) contain a population of neurons with saccade-related activity and a separate population with pursuit-related activity (Tian & Lynch, 1996; Heinen & Liu, 1997; Rosano *et al.* 2002). For the FEF, these two populations are located in different subregions. The LIP, which is interconnected with FEF and SEF, contains both saccade-related and pursuit-related neurons (Kurylo & Skavenski, 1991). In summary, the cortical networks subserving saccades and pursuit look similar, as confirmed by fMRI studies (Berman *et al.* 1999), but are largely based on different neuronal populations. From the cortex, several descending pathways convey information and motor commands to the ocular motoneurons.

The cortico-ponto-cerebellar (cortex – dorsolateral pontine nuclei – flocculus, paraflocculus and vermis) pathway was traditionally considered as the descending pathway of the smooth pursuit system. However, some areas within this pathway also contain saccade-related activity. For instance, the cerebellar vermis is involved in the control of both saccades and pursuit (Krauzlis & Miles, 1998; Takagi *et al.* 1998, 2000). In addition, recent experiments demonstrated that pursuit-related neurons in the dorsal pontine nuclei are also saccade related and sensitive to both position and velocity (Dicke *et al.* 2004). Moreover, the dorsolateral pontine nuclei receive afferents from the SC (Harting, 1977), a key structure in the position pathway controlling saccades. Another descending pathway, which conveys signals from the cerebral cortex to the SC (either directly or via the basal ganglia), primarily subserves the saccadic network.

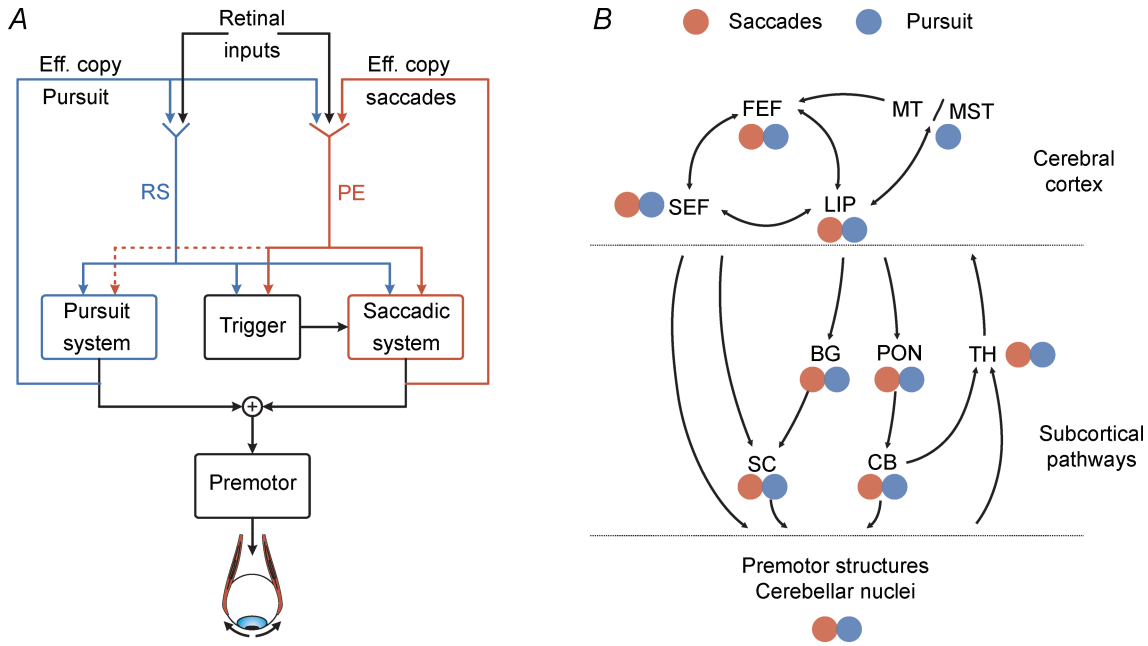

Figure 4. Model of the synergies between saccades and pursuit and brain circuitry subserving saccades and pursuit

A, the retinal inputs are processed into retinal slip (RS, blue lines) or position error (PE, red lines). In the absence of sensory inputs, RS is estimated from efference copies (Eff. copy pursuit) of the pursuit commands whereas PE is estimated from efference copies of both saccade (Eff. copy saccade) and pursuit commands. Estimates of position and velocity errors are sent to both saccadic and pursuit systems, which process them into motor commands. The minor role of the position input to the smooth pursuit system is represented by the red dash lines. The trigger uses these inputs to decide whether a catch-up saccade should be triggered. Pursuit and saccadic commands are then summed up and conveyed to the premotor structures. *B*, colours were assigned to each brain area following its involvement in each motor pathway (saccade- or pursuit-related activity; red or blue disks). BG: basal ganglia; CB: cerebellum; FEF: frontal eye field; LIP: lateral intraparietal area; MST: medial superior temporal area; MT: middle temporal area; PON: pontine nuclei; SC; superior colliculus; SEF: supplementary eye field; TH: thalamus.

However, the basal ganglia also contain pursuit-related neurons (Cui *et al.* 2003; Basso *et al.* 2005) and the SC provides a position signal to the smooth pursuit system (Basso *et al.* 2000; Krauzlis, 2003). Moreover, there is evidence that the SC codes the motor goal whatever the type of eye movement and not only the classical motor map of saccade endpoints (Krauzlis *et al.* 1997).

These pathways terminate either on cerebellar nuclei or on brainstem premotor circuits. These structures often contain saccade- and pursuit-related signals. For example, the fastigial oculomotor region (FOR), a cerebellar nucleus that receives the output of the vermis, does influence both pursuit and saccades. Neurons in FOR burst at the start of contraversive saccades and at the end of ipsiversive saccades and also show pursuit-related activity (Fuchs *et al.* 1993, 1994). In the pathway between SC and the oculomotor nuclei, several premotor areas contain both saccade- and pursuit-related neural activity. For instance, some neurons in the nucleus of the optic tract (NOT) fire during smooth pursuit and small saccades (Missal *et al.* 2002*a*). Moreover, brainstem premotor nuclei, which generate the burst of activity necessary to elicit a saccade (reviewed in Ramat *et al.* 2007), receive afferents from SC and from the saccadic and pursuit subregions of the FEF (Yan *et al.* 2001). They also contain some classes of neurons that are modulated during both saccades and pursuit. Among them, the omnipause neurons, which are known to inhibit the release of saccades, are also modulated during smooth pursuit eye movements (Missal & Keller, 2002). Consistently, large brainstem lesions impair both saccades and smooth pursuit (Bogousslavsky & Meienberg, 1987). Similarly, other premotor areas that control horizontal and vertical gaze respond to both saccades and pursuit (Chubb & Fuchs, 1982; Missal *et al.* 2000; Keller & Missal, 2003). From the cerebellar nuclei and the brainstem premotor circuits, the neural commands are conveyed to the oculomotor nuclei that innervate the extra-ocular muscles.

Finally, an ascending pathway that plays a central role in the feedback loop is included in both the saccadic and smooth pursuit systems. These feedback signals are mainly conveyed by the cerebellum and the thalamus, which has recently been shown to mediate saccadic and pursuit signals (Sommer & Wurtz, 2002, 2004*a*,*b*; Sommer, 2003; Tanaka, 2005).

In summary, the brain networks subserving oculomotor functions do not resemble the classical view of separate networks for saccades and pursuit (Petit & Haxby, 1999). In accordance with recent behavioural findings, the two brain networks rather seem intertwined (Krauzlis, 2004, 2005).

Conclusion

Classically, the oculomotor system was viewed as the juxtaposition of the saccadic and smooth pursuit systems. The experimental evidence of shared retinal inputs, common brain areas and synergies emphasizes that saccades and smooth pursuit are not subserved by distinct systems but are rather included in a more integrated system. Of course, in some cases, one or the other type of eye movement is better suited for the specified goal; hence saccades re-orientate gaze to stationary targets and smooth eye movements are restricted to track moving targets. However, in many circumstances, there is evidence that the central nervous system takes advantage of the complementary characteristics of both types of eye movements in order to optimize visual information. Smooth and saccadic eye movements reflect different modes in the trade-off between speed and accuracy during initiation and target selection. The brain monitors the smooth pursuit response in order to generate saccades when necessary. The synergy between saccades and pursuit increases the oculomotor performance in different contexts (tracking, target localization, prediction, target selection) and allows humans to perform skilled motor acts (like smashing a mosquito in flight).

Collaboration between saccades and pursuit gives a good opportunity to investigate how the central nervous system combines different modes of motor control to achieve a common goal. Indeed, saccadic and smooth pursuit systems are clearly much more integrated than has been classically proposed. This is compatible with the existence of a single controller that maximizes the performance of a common tracking goal, as has been reported recently in the fly (Boeddeker & Egelhaaf, 2005).

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Acknowledgements

This work was supported by the Fonds National de la Recherche Scientifique; the Fondation pour la Recherche Scientifique Médicale; the Belgian Program on Interuniversity Attraction Poles initiated by the Belgian Federal Science Policy Office; internal research grant (Fonds Spéciaux de Recherche) of the Université catholique de Louvain and the European Space Agency (ESA) of the European Union. The authors are grateful to Marcus Missal and Miriam Spering for their careful reading and valuable comments on an earlier version of the manuscript.